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Stable Periodic Orbits for a Predator–Prey Model with Delay

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In this paper we consider a predator–prey model with time lag which improves upon that proposed by Cavani and Farkas [1994, *Acta Math. Hungar*. **63**(3), 213–229]. We show that when the model has exactly one non-trivial unstable and hyperbolic equilibrium there exists a stable periodic orbit. © 2000 Academic Press

Key Words: predator–prey model; stable periodic orbit; delay; uniform persistence.

1. INTRODUCTION

In this paper we will consider a predator–prey model with delay and a non-constant death rate, described by the integro-differential system

$$
\begin{aligned}
N' &= N\left[\frac{\varepsilon}{K}(K-N) - \frac{aP}{\beta+N}\right],\\
P' &= P\left[-M(P) + b\int_{-\infty}^{t} \alpha \frac{N(\tau)}{\beta+N(\tau)} \exp(-\alpha(t-\tau))\,d\tau\right],
\end{aligned}
\tag{1.1}
$$

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where the exponential weight function satisfies

$$\int_{-\infty}^{t} \alpha \exp(-\alpha(t-\tau))\, d\tau = \int_{0}^{\infty} \alpha \exp(-\alpha s)\, ds = 1.$$

We are assuming in a more realistic fashion that the present level of the predator affects instantaneously the growth of the prey, but that the growth of the predator is influenced by the amount of prey in the past. More precisely, the number of predators grows depending on the weight-average time of the Michaelis–Menten function of N over the past by means of the function $Q(t)$ given by the integral

$$Q(t) := \int_{-\infty}^{t} \alpha \frac{N(\tau)}{\beta + N(\tau)} \exp(-\alpha(t-\tau))\, d\tau, \qquad \alpha > 0. \quad (1.2)$$

Clearly this assumption implies that the influence of the past fades away exponentially and the number $1/\alpha$ might be interpreted as the measure of the influence of the past. So, the smaller the $\alpha > 0$, the longer the interval in the past in which the values of N are taken into account; see [1, 3, 6].

$N(t)$ and $P(t)$ denote the quantities of prey and predators, respectively. $\varepsilon > 0$ is the specific growth rate of prey in the absence of predation and without environmental limitation. $K > 0$ is the carrying capacity of prey in the absence of predators. The functional response of the predator is of Michaelis–Menten or Holling type (see [4]) with satiation coefficient $a > 0$ and conversion rate $b > 0$. The specific mortality of predators is given by

$$M(P) = \frac{\gamma + \delta P}{1 + P} = \delta + \frac{\gamma - \delta}{1 + P}, \quad (1.3)$$

which depends on the quantity of predators. Here, $\gamma > 0$ is the mortality at low density and $\delta > 0$ is the limiting mortality, the natural assumption being that $0 < \gamma \leq \delta$. This model, introduced in [1], differs from more frequently used models in that the predator mortality is neither a constant nor an unbounded function; rather, it is increasing with the quantity of predators. When $\gamma = \delta$, system (1.1) without delay ($Q = N$) reduces to the classical predator–prey system with the Holling-type functional response which has been extensively studied. Hereafter, we assume that $\gamma < \delta$.

The integro-differential system (1.1) can be transformed into (see [2, 3]) the system of ordinary differential equations on the interval $[0, \infty)$,

$$N' = N\left[\left(1 - \frac{N}{K}\right)\varepsilon - \frac{aP}{\beta + N}\right], \quad (1.4)$$

$$P' = P[-M(P) + bQ], \quad (1.5)$$

$$Q' = \alpha\left[\frac{N}{\beta + N} - Q\right]. \quad (1.6)$$

We understand the relationship between the two systems as follows: If (N, P): $[0, \infty) \to \mathbb{R}^2$ is the solution of (1.1) corresponding to a continuous and bounded initial function $\tilde{N}$: $(-\infty, 0] \to \mathbb{R}$ and $P(0) = P_0$, then (N, P, Q): $[0, \infty) \to \mathbb{R}^3$ is a solution of (1.4)–(1.6) with $N(0) = \tilde{N}(0)$, $P(0) = P_0$, and

$$Q(0) = Q_0 = \int_{-\infty}^{0} \alpha \frac{\tilde{N}(\tau)}{\beta + \tilde{N}(\tau)} \exp(\alpha\tau)\, d\tau.$$

Conversely, if (N, P, Q) is any solution of (1.4)–(1.6) defined on the entire real line and bounded on $(-\infty, 0]$, then Q is given by (1.2) so (N, P) satisfies (1.1).

The main concern of this paper is to study the dynamics of the system (1.4)–(1.6). More concretely, we will show that when the problem (1.4)–(1.6) has just one non-trivial unstable and hyperbolic equilibrium there exists a stable periodic orbit.

2. PRELIMINARIES

In this section we will summarize the main facts related to our research. Let us consider the system of differential equations

$$x' = F(x), \qquad x \in D, \tag{2.1}$$

where D is an open subset on $\mathbb{R}^3$ and F is twice continuously differentiable in D. The noncontinuable solution of (2.1) satisfying $x(0) = x_0$ is denoted by $x(t, x_0)$, the positive (negative) semi-orbit through x_0 is denoted by $\varphi^+(x_0)$ $(\varphi^-(x_0))$, and the orbit through x_0 is denoted by $\varphi(x_0) = \varphi^-(x_0) \cup \varphi^+(x_0)$. We use the notation $\omega(x_0)$ $(\alpha(x_0))$ for the positive (negative) limit set of $\varphi^+(x_0)$ $(\varphi^-(x_0))$ provided the later semi-orbit has compact closure in D.

System (2.1) is said to be competitive in D if the Jacobian matrix of F at x, $F'(x)$, has non-positive off-diagonal elements

$$\frac{\partial F_i}{\partial x_j} \le 0, \qquad i \ne j,$$

at each point of D. System (2.1) is said to be competitive and irreducible in D provided that the Jacobian matrix is an irreducible matrix at each point $x \in D$ and (2.1) is competitive in D. Recall that an $n \times n$ matrix A is irreducible if for each nonempty proper subset I of $N = \{1, 2, \dots, n\}$ there exist $i \in I$ and $j \in N - I$ such that $A_{ij} \ne 0$.

For vectors x and y in $\mathbb{R}^3$ the inequality $x \ll y$ ($x \leq y$) means that $x_i < y_i$ ($x_i \leq y_i$) holds for all i and $x < y$ means that $x \leq y$ but $x \neq y$. Two vectors x and y are related if either $x \leq y$ or $y \leq x$ and are unrelated otherwise. The open set D is said to be p convex provided that for every x and y belonging to D for which $x \leq y$ the line segment joining x and y belongs to D.

The following theorem is proved in [7].

THEOREM 1. *Let* (2.1) *be a competitive system in* $D \subset \mathbb{R}^3$ *and suppose that D contains a unique equilibrium point p which is hyperbolic and assume that $F'(p)$ is irreducible. Suppose further that $W^s(p)$, the stable manifold of p, is one-dimensional. If $q \in D \setminus W^s(p)$ and $\varphi^+(q)$ has compact closure in D, then $\omega(q)$ is a nontrivial periodic orbit.*

The existence of an orbitally stable periodic solution can also be proved. We introduce the following hypotheses.

(H1) *System* (2.1) *is dissipative*: *For each $x \in D$, $\varphi^+(x)$ has compact closure in D. Moreover, there exists a compact subset B of D with the property that for each $x \in D$ there exists $T(x) > 0$ such that $x(t, x) \in B$ for $t \geq T(x)$.*

(H2) *System* (2.1) *is competitive and irreducible in D.*

(H3) *D is an open, p-convex subset of* $\mathbb{R}^3$.

(H4) *D contains a unique equilibrium point x^* and* $\det(F'(x^*)) < 0$.

The following result holds (see [8]):

THEOREM 2. *Let* (H1) *through* (H4) *hold. Then either*

(a) *x^* is stable or*

(b) *there exists a nontrivial orbitally stable periodic orbit in D. In addition, let us assume that F is analytic in D. If x^* is unstable then there is at least one but no more than finitely many periodic orbits for* (2.1) *and at least one of these is orbitally asymptotically stable.*

Our system (1.4)–(1.6) can be transformed into a competitive system. Let us set $u = (N, P, Q)^{\mathrm{T}}$, $v = (x, y, z)^{\mathrm{T}}$, and $H = \operatorname{diag}[1, 1, -1]$. The transformation $v = Hu$ in the system (1.4)–(1.6) results in

$$
\begin{aligned}
x' &= x\left[\left(1 - \frac{x}{K}\right)\varepsilon - \frac{ay}{\beta + x}\right],\\
y' &= y[-bz - M(y)],\\
z' &= -\alpha\left(\frac{x}{\beta + x} + z\right).
\end{aligned}
\tag{2.2}
$$

Let F denote the right-hand side of (2.2). Then the Jacobian of F is given by

$$F'(v) = \begin{bmatrix} a_{11} & -\dfrac{ax}{\beta + x} & 0 \\ 0 & a_{22} & -by \\ -\dfrac{\alpha\beta}{(\beta + x)^2} & 0 & -\alpha \end{bmatrix},$$

where a_{ii} are irrelevant for determining whether (2.2) is competitive or irreducible. Obviously, (2.2) is competitive and irreducible in the open region $D = \{(x, y, z) \in \mathbb{R}^3 : x > 0,\ y > 0,\ z < 0\}$. Our main results will follow from this observation and the above theorems.

3. LOCATION OF EQUILIBRIA AND DISSIPATIVENESS

For simplicity, let us rewrite (1.4)–(1.6) as

$$N' = \frac{a}{b} h(N)[f(N) - P], \qquad P' = P[bQ - M(P)],$$

$$Q' = \frac{\alpha N}{\beta + N} - \alpha Q,$$

where

$$f(N) = \frac{\varepsilon}{aK}(K - N)(\beta + N), \qquad M(P) = \frac{\gamma + \delta P}{1 + P}.$$

The equilibria of (1.4)–(1.6) consist of two trivial critical points $E_1 = (0, 0, 0)$ and $E_2 = (K, 0, K/(\beta + K))$ in the boundary of $\mathbb{E}$, the non-negative octant in $\mathbb{R}^3$, and a set of non-trivial critical points obtained as the intersection of the curves

$$P = f(N), \qquad Q = \frac{N}{\beta + N}, \qquad P = g(N) \equiv M^{-1}(h(N)) = c\frac{N - d}{e - N}, \tag{3.1}$$

where

$$c = \frac{b - \gamma}{b - \delta}, \qquad d = \frac{\beta\gamma}{b - \gamma}, \qquad e = \frac{\beta\delta}{b - \delta}, \qquad h(N) = \frac{bN}{N + \beta}.$$

Now it is apparent from the first and last equations of (3.1), which combine to give a cubic equation for N, that there exist at most three such nontrivial equilibria (N, P, Q). Observe that from (3.1) it follows that any nontrivial equilibrium has to satisfy the condition $0 < N < K$. Since we are interested in the case when $0 < \gamma < \delta$, we obtain that $b - \delta < b - \gamma$. So, we have the following cases:

(i) $0 < b - \delta < b - \gamma$,

(ii) $b - \delta < b - \gamma < 0$, and

(iii) $b - \delta < 0 < b - \gamma$.

Let us consider the case (i). A straightforward computation shows that $c > 0$, $0 < d < e$. Thus, if $d < K$ then there exists exactly one nontrivial equilibrium. To see this, note that an equilibrium value of N must satisfy

$$h(N) = M(P) \subset [\gamma, \delta) = [h(d), h(e))$$

so $d \leq N < e$ must be a root of $g(N) - f(N) = 0$. As the latter is negative at $N = d$ and has a vertical asymptote at $N = e$ there is at least one root. Since $g''(N) - f''(N) > 0$, there can be at most one root N_0, and $g'(N_0) - f'(N_0) > 0$. The latter holds since otherwise $g' - f' < 0$ for $d \leq N < N_0$, in which case there would be no root.

It is not difficult to prove that no nontrivial equilibria exist when $d \geq K$.

In the case (ii), we have that $c > 0$, $d < e < 0$, and $e < -\beta$ and therefore the system (1.1) has no nontrivial equilibria.

Finally, let us consider the case when $b - \delta < 0 < b - \gamma$. This condition implies that $c < 0$, $e < 0 < d$, and $e < -\beta$.

It is easy to check that $f(N^*) = \varepsilon(K + \beta)^2/4aK$, where $N^* = (K - \beta)/2$ is the abscissa of the parabola's vertex defined by (3.1). First, we shall show that under a suitable choice of parameters the system (1.1) has exactly three equilibria. Let us pick the parameter of the system (1.1) in such a way that

$$\frac{\varepsilon K}{4a} > -c, \qquad b > 2\gamma, \qquad 3\beta < K.$$

A straightforward computation shows that $d < \beta < N^*$, $f(N^*) \geq \varepsilon K/4a$, and $f(\beta) < g(\beta)$ for small enough positive β. Thus, there exists an $N_1 \in (d, \beta)$ such that $f(N_1) = g(N_1)$. Now, since $f(N^*) \geq \varepsilon K/4a > -c$, it follows that there exists an $N_2 \in (N_1, N^*)$ and an $N_3 > N^*$ such that $f(N_i) = g(N_i)$, $i = 2, 3$. This proves our assertion.

It is not difficult to deduce from the above analysis that in the third case the system (1.1) can have one, two, or three non-trivial equilibria. N_1 and

N_2 (N_2 and N_3) can collapse, thus generating a saddle–node bifurcation. Both trivial equilibria are saddles. For more details see [5].

The next theorem guarantees that the system (1.4)–(1.6) is biologically well behaved and that the dynamics of the system is concentrated on a bounded region of $\mathbb{R}^3$. Concretely, the following result holds:

THEOREM 3. *Let* $\mathbb{E} = \{(N, P, Q) \in \mathbb{R}^3 : N \geq 0,\ P \geq 0,\ Q \geq 0\}$; *then* $\mathbb{E}$ *is positively invariant under the flow induced by* (1.4)–(1.6). *Moreover*, (1.4)–(1.6) *is pointwise dissipative and the absorbing set* (*into which every solution eventually enters and remains*) *is given by* $B = [0, K] \times [0, M_1] \times [0, 1]$, *where* $M_1 = \varepsilon(\beta + K + 1)/a$.

Proof. Clearly the system (1.4)–(1.6) is equivalent to the integral equations

$$N(t) = N_0 \exp \int_0^t \left\{ \varepsilon \left[1 - \frac{N(s)}{K} \right] - \frac{aP(s)}{\beta + N(s)} \right\} ds,$$

$$P(t) = P_0 \exp \int_0^t \{ -M(P) + bQ \}\, ds,$$

$$Q(t) = Q_0 e^{-\alpha t} + \alpha \int_0^t \frac{N(s)}{\beta + N(s)} e^{\alpha(s-t)}\, ds.$$

These equalities certainly imply that the solutions of (1.4)–(1.6) remain in $\mathbb{E}$ as long as they are defined.

Now, let us prove that the solution of the system (1.4)–(1.6) are bounded for $t \geq 0$.

Taking into account that

$$w(t) = \frac{K}{1 + c_0 \exp(-\varepsilon t)}, \qquad c_0 = \frac{K - N_0}{N_0},$$

is the solution of the initial value problem

$$w' = \varepsilon w \left[1 - \frac{w}{K} \right], \qquad w(0) = N_0 > 0,$$

and using standard comparison arguments we get that

$$0 < N(t) \leq \frac{K}{1 + c_0 \exp(-\varepsilon t)}, \qquad t \geq 0.$$

This implies the boundedness of N on the interval $[0, \infty)$. Having in mind this fact and that α is positive, (1.6) gives us that $Q(t)$ is bounded for all $t \geq 0$. Moreover, for sufficiently small $\varepsilon^* > 0$, there exists a number $T_1 = T_1(\varepsilon^*, x_0) > 0$, $x_0 = (N_0, P_0, Q_0)$, such that

$$0 < N(t) < K + \varepsilon^*, \qquad 0 < Q(t) < 1 + \varepsilon^*, \qquad \forall t \geq T_1. \quad (3.2)$$

Let us prove the boundedness of $P(t)$. Taking into account (1.5) and the fact that $M(P) \geq \gamma$, we get

$$P'(t) \leq P(t)[-\gamma + bQ(t)]. \quad (3.3)$$

Let us show that there cannot exist a $T = T(M_1, x_0) > 0$ such that

$$P(t) \geq M_1, \qquad \forall t \geq T, \quad (3.4)$$

where

$$M_1 = \frac{\beta + K + 1}{a}\varepsilon.$$

Indeed, assume that (3.4) is true. Then, taking into account (3.2) and (3.4), we get that

$$\frac{aP(t)}{N(t) + \beta} \geq \varepsilon, \qquad \forall t \geq T^*,$$

where $T^* = \max\{T_1, T\}$. Then, from this and Eq. (1.4), we obtain

$$N'(t) = -\frac{\varepsilon}{K}N^2 + N\left[\varepsilon - \frac{aP(t)}{N(t) + \beta}\right] \leq -\frac{\varepsilon}{K}N^2(t), \qquad \forall t \geq T^*.$$

This immediately implies that

$$0 < N(t) \leq z(t) \to 0, \qquad \text{as } t \to \infty,$$

where $z(t)$ is the solution of the equation

$$z'(t) = -\frac{\varepsilon}{K}z^2(t), \qquad z(T^*) = N(T^*) > 0.$$

Having in mind that $N(t) \to 0$ as $t \to \infty$ and the equation (1.6), we get that $Q(t) \to 0$ as $t \to \infty$, as well. Henceforth, there exists $t_0 \geq T^*$ such that

$$Q(t) \leq \gamma/2, \qquad \forall t \geq t_0. \quad (3.5)$$

Now taking into account (3.3) and (3.5), we get

$$P'(t) \le -\frac{\gamma}{2}P(t), \qquad \forall t \ge \tau = \max\{t_0, T^*\},$$

which implies that $\lim_{t\to\infty} P(t) = 0$, a contradiction.

Let us define the function $\varphi(t) = P(t) - M_1$. We have to consider two possibilities. If there is some t_0 such that $\varphi(t) \ne 0$ for any $t > t_0$, we say that the zeroes of φ are bounded. If this is not true we say that the zeroes are unbounded; in this case $\varphi(t) = 0$ for a sequence of t_n tending to $+\infty$ as $n \to \infty$.

If the zeroes of $\varphi(t)$ are bounded then $0 < P(t) \le M_1$ for any $t \ge t_0$.

If the zeroes are unbounded the t-axis is divided by the zeroes into a sequence of intervals J_n, $n \ge 1$. In each such interval $\varphi(t)$ is of constant sign. Let us assume that $\varphi(t) \ge 0$ for $t \in J_n$, $n = 1, 3, 5, \dots$. Since $P(t) \ge M_1$ on the intervals J_{2n-1}, arguing as in the proof that (3.4) is not possible, we obtain that $P'(t) \le -(\gamma/2)P(t) < 0$ for $t \in J_{2n-1}$ and n large enough. Thus, $P(t) \le P(t_{2n-1}) = M_1$, $\forall t \in J_{2n-1}$ and n large enough. This contradiction completes the proof of our claim. ∎

4. EXTINCTION OF THE PREDATOR AND UNIFORM PERSISTENCE

Hereafter in this paper we restrict our attention to the case (i), $0 < \gamma < \delta < b$. The goal of this section is to give conditions implying that the predator and prey persist indefinitely, i.e., that neither becomes extinct. First, we identify a less interesting case where the predator cannot survive.

PROPOSITION 4. *If $d > K$, then*

$$\lim_{t\to\infty} P(t) = 0$$

for every solution of (1.4)–(1.6).

Proof. It is easily seen that $\limsup_{t\to\infty} N(t) \le K$ and from this to deduce that $\limsup_{t\to\infty} Q(t) \le K/(\beta + K)$. If $\eta > 0$ is arbitrary, there exists $T = T(\eta)$ such that $Q(t) \le K/(\beta + K) + \eta$ for $t > T$. Hence, for $t > T$ we have

$$P' \le P\left(-\gamma + \frac{bK}{\beta + K} + \eta\right).$$

Our hypothesis says that by choosing η small enough $-\gamma + bK/(\beta + K) + \eta < 0$. The desired conclusion follows by a standard comparison result. ∎

One can actually show that E_2 attracts all solutions starting in the interior of $\mathbb{E}$ (and even when $d = K$) with additional work. The conclusion of the proposition also holds in the case (ii) since $b < \gamma$ and $P' \leq P(-\gamma + b)$.

For the remainder of this paper we will assume that $d < K$. A straightforward computation shows that $c > 0$, $0 < d < e$. In this case there exists just one nontrivial equilibrium $E^* = (N_0, P_0, Q_0)$, where

$$P_0 = f(N_0), \qquad Q_0 = \frac{N_0}{\beta + N_0}, \qquad P_0 = M^{-1}\left(\frac{bN_0}{\beta + N_0}\right) = c\frac{N_0 - d}{e - N_0}.$$

The stability properties of E_1 and E_2 can be determined by their linearizations. Let $J(E_i)$ denote the Jacobian matrices evaluated at E_i. Then

$$J(E_1) = \begin{pmatrix} \varepsilon & 0 & 0 \\ 0 & -\gamma & 0 \\ \dfrac{\alpha}{\beta} & 0 & -\alpha \end{pmatrix}$$

and

$$J(E_2) = \begin{pmatrix} -\varepsilon & -\dfrac{aK}{\beta + K} & 0 \\ 0 & -\gamma + \dfrac{bK}{\beta + K} & 0 \\ \dfrac{\alpha\beta}{(\beta + K)^2} & 0 & -\alpha \end{pmatrix}.$$

Thus, E_1 is a saddlepoint, unstable to invasion by the prey, having two negative eigenvalues and one positive eigenvalue. E_2, also a saddlepoint with two negative eigenvalues and one positive eigenvalue, is unstable to invasion by the predators. The following lemma summarizes the behavior of the solutions of (1.4)–(1.6) on $\partial\mathbb{E}$ and identifies the two-dimensional stable manifolds of the E_i.

LEMMA 5. *Assume that $K > d$. Then*

(i) *The N-axis, the Q-axis, the (N, Q)-plane, and the (P, Q) plane are invariant under the flow induced by* (1.4)–(1.6).

(ii) *The intersection of the stable manifold of* E_1 *with* $\mathbb{E}$ *consists of all points* $(0, P, Q)$ *such that* $P \geq 0$ *and* $Q \geq 0$.

(iii) *The intersection of the stable manifold of* E_2 *with* $\mathbb{E}$ *consists of all points* $(N, 0, Q)$ *with* $N > 0$ *and* $Q > 0$.

Proof. The statements (i) and (ii) are obvious. To prove (iii) note that all solutions of the system

$$N' = \varepsilon N\left[1 - \frac{N}{K}\right], \qquad Q' = \alpha\left[\frac{N}{\beta + N} - Q\right]$$

satisfy $N \to K$ and $Q \to K/(\beta + K)$ as $t \to \infty$. ∎

We now show that the predator and the prey persist indefinitely if $K > d$. Mathematically, we use the theory of uniform persistence (see [9]).

THEOREM 6. *Assume that* $K > d$. *Then there exists* $\eta > 0$ *such that*

$$\liminf_{t \to \infty} N(t) > \eta$$

and

$$\liminf_{t \to \infty} P(t) > \eta$$

for all solutions of (1.4)–(1.6) *starting in* $\mathbb{E}$ *for which* $\mathbb{P}(0) > 0$.

Proof. We use Theorem 4.6 of [9], employing the notation of that result and the notation $u = (N, P, Q)$. Let $X_1 = \{u \in \mathbb{E} : N > 0,\ P > 0\}$ and $X_2 = \{u \in \mathbb{E} : N = 0 \text{ or } P = 0\}$. We need to prove that solutions starting in X_1 are eventually bounded away from X_2, uniformly with respect to the initial data. The compactness assumption $(C_{4,2})$ of Theorem 4.6 holds with B as in Theorem 2 (for small positive δ as defined in [9]). Define $\Omega_2 = \cup_{u \in X_2} \omega(u)$. According to Lemma 4, Ω_2 consists of the equilibria E_1 and E_2 and hence it has an acyclic isolated covering $M = M_1 \cup M_2$, where $M_i = \{E_i\}$ for $i = 1, 2$. Here, acyclity of M means that there do not exist points $u_i \in X_2$ with $\alpha(u_1) = E_1$, $\omega(u_1) = E_2$, $\alpha(u_2) = E_2$, and $\omega(u_2) = E_1$. In fact, it is the latter (u_2) which cannot exist by Lemma 4. Isolatedness of M_i means that these sets are isolated in $\mathbb{E}$, that is, there exist open sets U_i of M_i in $\mathbb{E}$ such that M_i is the maximal invariant set in U_i. This holds since each E_i is hyperbolic. We must also show that each M_i is a weak repeller for X_1: for all $u(0) \in X_1$, $\limsup_{t \to \infty} |u(t) - E_i| > 0$. Suppose, for contradiction, that a solution $u(t)$ with $u(0) \in X_1$ satisfies $\lim_{t \to \infty} u(t) = E_1$. Then $u(0)$ belongs to the stable manifold of E_1. But the intersection of the latter with $\mathbb{E}$ consists of the (P, Q)-plane by Lemma 4 so we have a contradiction to $u(0) \in X_1$. An entirely similar contradiction is reached if $\lim_{t\to\infty} u(t) = E_2$ since the intersection of the stable manifold of E_2 with $\mathbb{E}$, as described in Lemma 4(iii), contains no points of X_1. Hence, by Theorem 4.6 of [9], X_2 is a strong repeller for X_1. ▮

5. STABILITY OF THE NONTRIVIAL EQUILIBRIUM

We want to determine the stability of the unique nontrivial equilibrium E^* in the case $0 < \gamma < \delta < b$ and $K > d$. It is convenient to examine the equivalent problem of the stability of the unique nontrivial equilibrium $v^* = HE^*$ of (2.2). The Jacobian matrix of F evaluated in the rest point is given by

$$F'(v^*) = \begin{bmatrix} \frac{a}{b}h(N_0)f'(N_0) & -\frac{a}{b}h(N_0) & 0 \\ 0 & -P_0M'(P_0) & -bP_0 \\ -\frac{a}{b}h'(N_0) & 0 & -\alpha \end{bmatrix},$$

and the characteristic equation is given by

$$P_\alpha(\lambda) = \lambda^3 + a_1(\alpha)\lambda^2 + a_2(\alpha)\lambda + a_3(\alpha),$$

where

$$a_1(\alpha) = \alpha + P_0M'(P_0) - \frac{a}{b}h(N_0)f'(N_0),$$

$$a_2(\alpha) = \alpha\left[P_0M'(P_0) - \frac{a}{b}h(N_0)f'(N_0)\right] - \frac{a}{b}h(N_0)f'(N_0)P_0M'(P_0),$$

$$a_3(\alpha) = \alpha\frac{a}{b}P_0h(N_0)\left[-f'(N_0)M'(P_0) + h'(N_0)\right].$$

It is worth noting that the coordinates of the critical point v^* are independent of α.

LEMMA 7.

$$\det F'(v^*) = -a_3 < 0.$$

Exactly one of the following hold:

(a) $\Re\lambda < 0$ *for all eigenvalues*.

(b) *There is one negative eigenvalue and a pair of nonzero purely imaginary eigenvalues* (*if and only if* $a_1 > 0$, $a_2 > 0$, *and* $a_1a_2 = a_3$).

(c) *There is one negative eigenvalue and a pair of eigenvalues with positive real part.*

Proof. We have

$$\begin{aligned} -f'(N_0)M'(P_0) + h'(N_0) &= M'(P_0)\left(\frac{h'(N_0)}{M'(P_0)} - f'(N_0)\right) \\ &= M'(P_0)(g'(N_0) - f'(N_0)) \\ &> 0, \end{aligned}$$

where $g(N) = M^{-1}(h(N))$ and where we've used that $g'(N_0) > 0$ from Section 3. Thus, $a_3 > 0$.

As the product of the eigenvalues is negative, we conclude that an even number (0 or 2) of eigenvalues have positive real part and zero cannot be an eigenvalue. In the nonhyperbolic case (b), one sees that $\eta^2 = a_2 = a_3/a_1$ by substituting $\lambda = -\eta i$ into $P(\lambda) = 0$. ∎

The Routh–Hurwitz criteria give necessary and sufficient conditions for (a). We will be particularly interested in finding sufficient conditions for v^* to be hyperbolic and unstable because Theorem 2 implies the existence of periodic orbits. Of course, the Hopf Bifurcation Theorem may apply but it leads to the existence of small-amplitude periodic orbits.

Let us define the function

$$\psi(\alpha) = a_1(\alpha)a_2(\alpha) - a_3(\alpha) = A\alpha^2 + B\alpha + C,$$

where

$$A = P_0 M'(P_0) - \frac{a}{b}h(N_0)f'(N_0),$$

$$B = A^2 - \frac{a}{b}h(N_0)h'(N_0)P_0,$$

$$C = -A\frac{a}{b}h(N_0)f'(N_0)P_0 M'(P_0).$$

Assume first that $f'(N_0) > 0$, i.e., the equilibrium v^* is in the Allee zone. Then dependence of the eigenvalues on the parameter α is as follows.

PROPOSITION 8. *Assume that $f'(N_0) > 0$.*

(i) *If $A < 0$, then v^* is hyperbolic and unstable with a one-dimensional stable manifold for all $\alpha > 0$.*

(ii) *If $A > 0$ then there exists $\alpha_0 > 0$ such that v^* is hyperbolic and unstable with a one-dimensional stable manifold for all $\alpha \in (0, \alpha_0)$ where*

$P_{\alpha_0}(\lambda)$ has a negative root and a pair of pure imaginary roots and all the roots of $P_\alpha(\lambda)$ have negative real part for all $\alpha > \alpha_0$.

Proof. If $A < 0$, then $a_2 < 0$ so the case (c) of Lemma 7 holds. If $A > 0$, then $a_1 > 0$ and $C < 0$. Also, $a_2(\alpha)$ is strictly increasing, negative for small α, and positive for large α. Case (c) holds while $a_2 < 0$ and so long as $\psi(\alpha) < 0$. As $A > 0$, ψ is eventually positive so case (a) holds for large α. ∎

The following example shows that both of the possibilities stated in Proposition 8 are feasible.

EXAMPLE 1. (i) Let us pick $\varepsilon = 1$, $a = 1$, $K = 1$, $\beta = 0.1$, $\gamma = 2$, $\delta = 2.9$, and $b = 3$. Under this selection of parameters the critical point is given by $(N_0, P_0) = (0.2711111205, 0.2704987688)$, $A = -0.1105504528$, and $f'(N_0) > 0$. In this parameter configuration $v^* = (N_0, P_0)$is hyperbolic with a one-dimensional stable manifold for any $\alpha > 0$.

(ii) Choosing $\varepsilon = 1$, $a = 1$, $K = 1$, $\beta = 0.1$, $\gamma = 0.2$, $\delta = 2$, and $b = 2.5$, the critical point is given by $(N_0, P_0) = (0.01833391485, 0.116164391)$, $A = 0.0340783025$, and $f'(N_0) > 0$. In this parameter configuration $v^* = (N_0, P_0)$ is hyperbolic with a one-dimensional stable manifold just for $\alpha \in (0, 9.397244481)$.

We have the following sufficient conditions for Case (i) of Proposition 8 to hold.

Remark 1. If $K - \beta > 2e$, then $f'(N_0) > 0$ and we might expect that $A < 0$ if $\delta - \gamma \ll 1$. Indeed,

$$A < \frac{\delta - \gamma}{4} - \frac{\varepsilon\gamma}{bK}(K - \beta - 2e),$$

so $A < 0$ if

$$\frac{\delta - \gamma}{\gamma} < \frac{4\varepsilon}{bK}(K - \beta - 2e).$$

Proof. It's easy to see that $P_0 M'(P_0) \leq (\delta - \gamma)/4$. Also, $h(N_0) > h(d) = \gamma$. ∎

Applying the Routh–Hurwitz criteria, we get the following result in the case $f'(N_0) < 0$:

PROPOSITION 9. *Let us assume that $f'(N_0) < 0$. Then $A > 0$, $C > 0$, and $a_i > 0$ for $i = 1, 2, 3$. Exactly one of the following holds*:

1. *All the roots of $P_\alpha(\lambda)$ have a negative real part for all $\alpha > 0$.*

2. *There exist* $0 < \alpha_1 \le \alpha_2$ *such that for* $\alpha \in (0, \alpha_1) \cup (\alpha_2, \infty)$ *the roots of* $P_\alpha(\lambda)$ *have negative real part, and* $P_\alpha(\lambda)$ *has a negative root and two complex roots with positive real part for all* $\alpha \in (\alpha_1, \alpha_2)$.

Case 2 *holds if and only if* $B < 0$ *and* $4AC < B^2$.

EXAMPLE 2. (i) Let us pick $\varepsilon = 1$, $a = 1$, $K = 1$, $\beta = 0.1$, $\gamma = 2.5$, $\delta = 2.9$, and $b = 2.91$. Under this selection of parameters the critical point is given by $(N_0, P_0) = (0.7543430654, 0.2098752985)$, $B = 0.2798963236$, and $f'(N_0) < 0$. In this case all roots of the characteristic equation have negative real part.

(ii) Choosing $\varepsilon = 1$, $a = 1$, $K = 1$, $\beta = 0.1$, $\gamma = 2$, $\delta = 2.5$, and $b = 2.51$, the critical point is given by $(N_0, P_0) = (0.5338977118, 0.295461174)$, $B = -0.164777546$, and $f'(N_0) < 0$. In this parameter configuration $v^* = (N_0, P_0)$ is hyperbolic with a one-dimensional stable manifold for any $\alpha \in (0.2971353469, 0.4186839291)$.

6. EXISTENCE OF A STABLE PERIODIC ORBIT

Our main result below gives sufficient conditions that almost every solution is asymptotically periodic.

THEOREM 10. *Let* $0 < \gamma < \delta < b$ *and* $K > d$ *hold. Assume that the unique nontrivial equilibrium* E^* *is hyperbolic and unstable. Then it has a one-dimensional stable manifold* $W^s(E^*)$. *Furthermore, there exists an asymptotically orbitally stable periodic orbit, and the omega limit set of every solution* $(N(t), P(t), Q(t))$ *with* $N(0) > 0$, $P(0) > 0$, *and* $(N(0), P(0), Q(0)) \notin W^s(E^*)$ *is a nonconstant periodic orbit.*

Proof. We apply Theorem 2 and Theorem 1 to the transformed system (2.2). From Lemma 7 we see that the stable manifold of E^* is one-dimensional. The existence of an orbitally asymptotically stable periodic orbit follows from Theorem 2 and the analyticity of the vector field. Note that (H1) holds by Theorem 2 and Theorem 6 (the latter must be translated appropriately to system (2.2)). In particular, we take the domain D as in Section 2. Using Theorem 6, Theorem 1 implies the final assertion. ∎

If $f'(N_0) > 0$, then E^* is hyperbolic and unstable for all small α (all α if $A < 0$). Since the "delay" is $1/\alpha$, stable periodic orbits exist for large delays and for all values of the delay if $A < 0$.

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